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Notes on Reproduction of a Tropical Pulmonate Limpet, *Siphonaria gigas* (Sowerby)

by

SALLY C. LEVINGS[1] AND STEPHEN D. GARRITY[2]

Smithsonian Tropical Research Institute, Box 2072, Balboa, Republic of Panama

Abstract. *Siphonaria gigas* (Sowerby, 1825) is one of the most abundant mollusks on exposed rocky shores of the Pacific coast of Panama. Egg rings are laid on the rock throughout most of the year, although fewer are laid during the dry season (approximately January to March). Egg rings are deposited with a marked lunar periodicity; significantly more are found during neap than spring tides. Unless placed in a microhabitat protected from fishes, egg rings are quickly eaten. The overall pattern of reproduction is similar to that reported for other tropical members of the genus.

INTRODUCTION

ALTHOUGH the seasonal pattern and cues for spawning have been described for many temperate limpets and limpetlike pulmonates, information on the reproductive biology of tropical species is sparse (review in BRANCH, 1981). We have had the opportunity to gather information on the reproductive biology of the tropical pulmonate limpet *Siphonaria gigas* (Sowerby, 1825) during several years of study on the Pacific coast of Panama. *Siphonaria gigas* is one of the most abundant mid-intertidal zone species in Panama (LEVINGS & GARRITY, 1984).

Siphonaria gigas ranges from Ecuador to Baja California (KEEN, 1971). It occurs on exposed rocky shores (KEEN, 1971; LEVINGS & GARRITY, 1984) and can reach a shell length of 70–80 mm, making it the largest bodied member of its genus (HUBENDICK, 1945). Like other Siphonariidae, *S. gigas* is a simultaneous hermaphrodite. Individual animals exchange spermatophores before cementing gelatinous egg rings to the rock. Eggs mature after about 7 days and veligers are released into the plankton; settlement occurs after 5–7 days (R. Emlet, personal communication). Here, we summarize our observations on the reproductive biology of *S. gigas* and compare it to that of other pulmonate limpets.

METHODS

Most observations were made on the inner Panama Bay islands of Taboguilla, Urava, Culebra, Flamenco, and Farallon between 1977 and 1985. Comparative data were taken throughout the Pearl Archipelago, in the Gulf of Chiriqui, and along the Darien coast. The intertidal community of this region has been described elsewhere (GARRITY & LEVINGS, 1981; LUBCHENCO *et al.*, 1984).

Seasonal and lunar patterns of reproductive behavior were determined by noting the presence or absence of egg rings or mating behavior in the field. Although this was done incidental to other work, records exist for all months of the year, except August, over an 8-yr period.

To determine the minimum size of reproductive maturity and to explore spatial relationships between pairs engaging in spermatophore transfer, the shell lengths and home scar locations of mating pairs were recorded. To estimate egg output, we counted the number of eggs in 10 randomly chosen 1 × 1 × 5-mm excised segments from each of seven freshly laid egg rings (rings collected 17 May 1978, Culebra). We measured the total length of an egg ring, then combined these data with the counts of eggs per 5-mm segment to estimate roughly the number of eggs in an "average-sized" egg ring. The inner and outer diameter, the number of whorls, and the distance from the nearest adult were measured on egg rings sampled from two bouts of deposition on Culebra in April and May 1978. To determine whether more than one egg ring could be laid during a single spawning period, we counted all egg rings and limpets of adult size on an isolated rock outcrop after a large bout of egg ring deposition.

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[1] Present address: Department of Zoology, University of Rhode Island, Kingston, RI 02881, U.S.A.

[2] Present address: Department of Zoology, University of Massachusetts, Amherst, MA 01003, U.S.A.

To estimate the degree of predation on egg rings, egg rings were measured, the number of whorls recorded, and the percentage of the egg ring destroyed was estimated visually. When portions of an egg ring are eaten, the base is still visible and total size can be estimated (see Figure 1). These data were compared for egg rings located in microhabitats exposed to fishes (*e.g.*, horizontal, sloping and vertical surfaces) and those protected from fishes (*e.g.*, in crevices or depressions). Incidental notes were made on damage to eggs at other sites and on species that damaged egg rings.

To determine whether damage to egg rings was due to predators other than fishes, rates of damage for egg rings under cages (n = 4, 50 × 50 × 5-cm cages, 1-cm mesh), roofs (n = 4, 50 × 50-cm roofs, 1-cm mesh, two sides open), and in open quadrats (n = 8, 50 × 50-cm quadrats) were compared (Taboguilla Island, November 1977). Egg rings under cages were protected from mollusks, fishes, and crabs greater than 1 cm in the narrowest dimension; those under roofs were exposed to mollusks, crabs, and to fishes that could feed under roofs 5 cm off the substrate. Open quadrats were exposed to mollusks, fishes, and crabs.

RESULTS

Either spermatophore transfer or egg ring deposition was observed in all months except February in at least one year (August not sampled, Table 1). Egg rings were found on fewer than 33% of the observation days during the dry season (conservatively defined as January to March, n = 32 records). In contrast, we found eggs in more than half the observation days during all other months (n = 81). The bouts of egg deposition in the early wet season (April and May) in inner Panama Bay produced the largest numbers of egg rings observed in that area (>1 egg ring/adult limpet). Large numbers of egg rings were occasionally observed at other sites (*e.g.*, Uva, 5 December 1981, approximately 0.7 egg ring/adult).

Along a stretch of shore, subpopulations were often in different stages of the reproductive cycle. Egg rings might be found in only one of a number of nearby sites. For example, from 9 to 11 November 1977, eggs were found on two sections of shore on Taboguilla, but were not present on two other areas surveyed. However, on 24 October 1982, we sampled 14 islands throughout the Perlas Archipelago. Egg rings were being deposited on 12 of 14 islands. Thus, some level of synchronization is possible. We were more than twice as likely to find egg rings during neap tides (second and fourth quarter of the moon) than spring tides (G test, $P < 0.001$).

Spermatophore transfer occurred less than two weeks before egg ring deposition. Transfer occurred on falling tides, when the limpets were still being washed. In 59 of 86 cases on 29 May 1979 (Taboguilla), individuals mated with animals unambiguously identified as their nearest neighbors; often the scars of nearest neighbors are so close

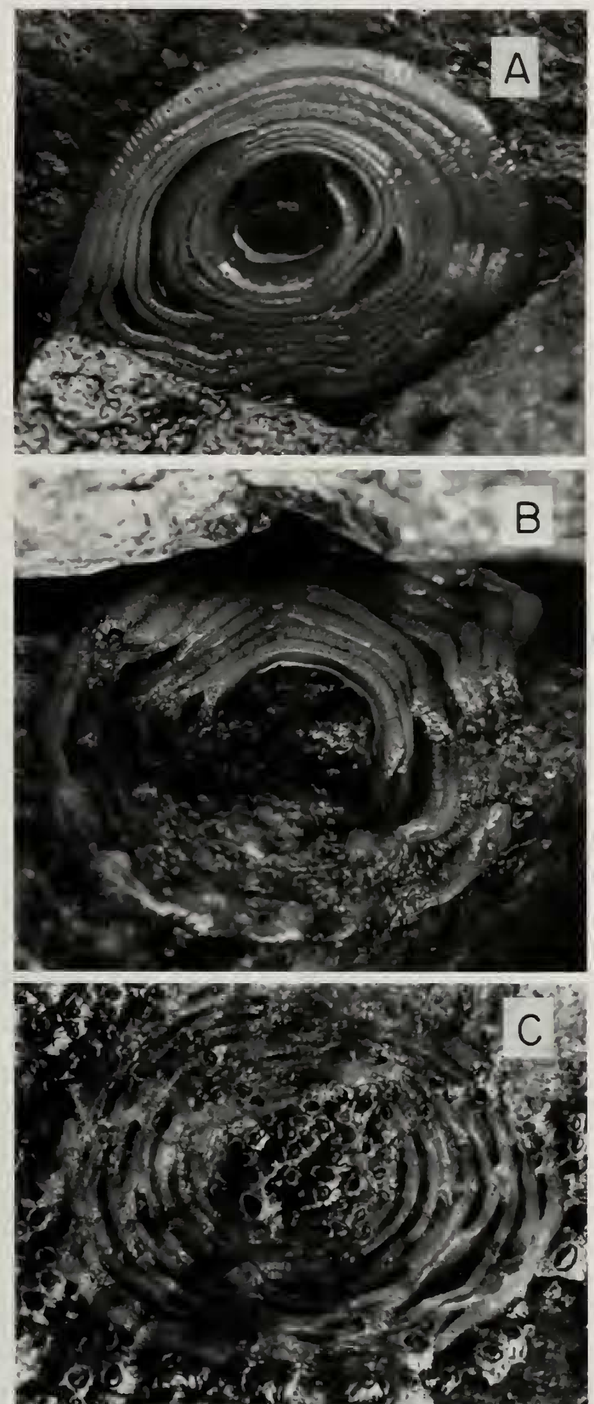

Figure 1

A. Fresh egg ring of *Siphonaria gigas*. B. Egg ring partially destroyed. Only the part of the egg ring inside the crevice remains. C. Egg ring on a homogeneous surface. Only the basal portion of the ring remains and bitemarks are visible. All rings approximately 70 mm in diameter. Culebra Island, May 1978.

Table 1

Egg ring deposition records, 1977–1985, for *Siphonaria gigas*.

Month	No. records	Proportion with eggs present
January	17	0.59
February	2	0
March	13	0.08
April	7	0.71
May	10	0.50
June	11	0.27
July	9	0.78
August	no data	—
September	4	0.75
October	19	0.84
November	5	0.60
December	16	0.57

Table 2

Amount of damage to *Siphonaria gigas* egg rings exposed to different types of consumers.*

	Number of rings		
	Undis-turbed	Dam-aged†	Total
Site 1			
In cages (n = 2)	11	0	11
Under roofs (n = 2)	5	0	5
In marked plots (n = 4)	6	14	20
Site 2			
In cages (n = 2)	4	1	5
Under roofs (n = 2)	11	0	11
In marked plots (n = 4)	5	17	22
Total			
Under cages or roofs (n = 8)	31	1	31
In open plots (n = 8)	11	31	42

* Data are the number of damaged *vs.* undamaged egg rings laid in cages, under roofs, or in open quadrats. Sites were sections of the shoreline of Taboguilla Island approximately 300 m apart. Sample date 9 November 1977. See text for further explanation.

† Egg rings were counted as damaged if they were disturbed in any way. In practice, damaged rings in the open quadrats were usually almost completely destroyed.

together that the limpets' shell edges are in contact. We never observed more than 20% of the adult population transferring spermatophores during a tidal cycle. Sizes of mating individuals were positively correlated ($r^2 = 0.31$, $P < 0.001$, n = 156 pairs, mean size = 43.2 mm, range 29–63, data from 23 May 1978 and 29 May 1979 on Taboguilla). This appeared to be due to the relatively narrow range of adult sizes and a weak tendency for nearest neighbors to be similar in size. No individual smaller than 29 mm in shell length was observed in reproductive behavior. In an undisturbed population, this size represents an individual approximately two years old (Levings & Garrity, unpublished data).

Egg rings consisted of a jellylike ribbon (approximately 5 mm high × 1 mm wide) laid out on the rock in a continuous ellipsoidal spiral (Figure 1). While laying, limpets stayed in one spot and rotated slowly while extruding the ribbon of eggs; egg rings thus have an empty ellipse in the center where the limpet's foot rested. A ring was deposited over a single low tide and might be laid either during the day or at night. Although individual *Siphonaria gigas* are greater than 15 cm from a conspecific only 0–14% of the time in nine population samples (Levings & Garrity, submitted), egg rings were on average 16.8 ± 1.2 cm (mean ± 1 SE) from the nearest adult. Limpets moved away from their home scars to deposit egg rings and most were placed in crevices or on vertical walls.

The average number of whorls in a ring was 8.2 ± 0.2 (mean ± 1 SE, range 2–12 whorls, n = 148 egg rings, 30 April and 17 May 1978, Culebra). The maximum outside diameter of an egg ring ranged from 31 to 85 mm; when uncoiled, the ribbon of eggs was up to 100 cm long. Rings were about 20% longer than wide (mean length = 49.6 ± 0.8 mm, mean width = 41.9 ± 0.7 mm, outer dimensions). The inner ellipse was similar in shape (mean length = 19.5 ± 0.5 mm, mean width = 16.7 ± 0.4 mm, mean area = 2.7 ± 0.1 cm^2). Each egg had a separate membrane and contained one veliger. Lengths of egg ring 1 × 1 × 5 mm contained an average of 78 eggs (range 54–115 eggs; each value is the average of 10 counts from each of 7 rings). Combining these measurements, an average-sized egg ring contained more than 75,000 eggs.

During one spawning period, a single limpet could lay more than one egg ring. On 17 May 1978, 130 limpets greater than 20 mm in shell length laid 161 egg rings on an isolated rock outcrop on Culebra; no egg rings were present on 16 May. Similarly high numbers were observed occasionally at other sites. At sites we often visited, several bouts of oviposition were observed during the year; thus, individuals can lay more than one egg ring during one spawning period and there are multiple spawning periods during the year.

Egg rings not located in protected microhabitats were heavily damaged (median percent damage, exposed microhabitats = 55%, range 20–95%, n = 22, protected microhabitats = 0%, range 0–75%, n = 70, Culebra, 17 May 1978). One of 32 egg rings under cages or roofs was damaged, while 31 of 42 of those located in open quadrats were almost completely destroyed (Table 2). If an egg ring was partially in a crevice, only the fraction on open substrate was damaged (Figure 1). Most damage was probably due to fishes because crevices were accessible to crabs and mollusks. Damage occurred during high tide, bitemarks were found on most damaged rings (*e.g.*, Figure 1), and there was usually a small amount of the base of the ring remaining. Egg rings located entirely in the open were essentially destroyed within two days of deposition.

Egg rings are rarely eaten by the predaceous gastropod *Purpura columellaris* (n = 10 observations in 1039 prey records, 6711 snails examined) and may be dislodged or bulldozed by *Chiton stokesi* (mean percent damaged = 20.6, range 5–33, n = 5 rings measured). *Pachygrapsus conversus,* an abundant and active crab (LUBCHENCO *et al.,* 1984), was observed probing rings on several occasions and may have eaten some eggs. Its effects, and those of mollusks, are likely to be of minor importance relative to the effects of fishes.

DISCUSSION

Reproduction in other *Siphonaria* has mostly been examined for temperate seas (see CREESE, 1980a; BRANCH, 1981, for review). Eggs tend to be deposited in spring and summer; lunar cycles are strongly marked. In *Siphonaria japonica* (Japan), *Siphonaria atra* (Palao), and *Siphonaria sipho* (Palao), eggs are laid during the second and fourth quarters of the moon (HIRANO, 1980; HIRANO & INABA, 1980; Abe, 1939, cited in ABE, 1940). We found this same pattern in *Siphonaria gigas.* The tropical species of *Siphonaria* also have extended breeding seasons (*Siphonaria pectinata, Siphonaria alternata* [ZISCHKE, 1974], *Siphonaria hispida* [MARCUS & MARCUS, 1966]). The basic breeding biology of *S. gigas* is similar to that of its conspecifics.

Most *Siphonaria gigas* probably deposit more than one egg ring during a spawning season, and may do so during a single period of spawning. However, with the data at hand, we cannot estimate fecundity either per spawning bout or per season for individual limpets; as in many species, egg ring size and number probably increase with limpet size (BRANCH, 1981). In general, *Siphonaria* appears to produce more eggs than co-occurring acmaeid limpets (CREESE, 1980a, b).

Egg rings in Panama are under strong predation pressure, as are gastropods on exposed surfaces (BERTNESS *et al.,* 1981; GARRITY & LEVINGS, 1983). If egg rings are not deposited in microhabitats where fishes cannot feed, they are quickly consumed. Other types of predators eat egg rings occasionally, but do not appear to have substantial effects. We have not been able to locate reports of fish predation on the egg rings of other Siphonariidae, so we do not know how widespread this phenomenon is.

We have suggested that egg rings are deposited in protected microhabitats to avoid destruction by predaceous fishes (Table 2). Alternatively, placement could be due to avoidance of heat stress and (or) desiccation. CREESE (1980a) transplanted egg rings of *Siphonaria denticulata* to both low and high tidal heights on the shore both in and out of tidepools. He showed that two-thirds of the rings placed in exposed microhabitats failed to hatch, while eggs in the other three microhabitats almost all hatched. He attributed losses to desiccation. Egg rings on exposed surfaces in Panama are rapidly consumed; they might also succumb to physical stress (GARRITY, 1984) if predators were not present. *Siphonaria gigas* ranges from Baja California to Ecuador; the activities of fishes must vary over this geographical range. In areas where fishes do not eat egg rings, physical stress could still affect rings laid in open microhabitats and might have been the driving force behind the evolution of placement in protected microhabitat.

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